



Pollination of Western Prairie Fringed Orchid, *Platanthera praeclara* Sheviak & Bowles: implications for restoration and management

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Introduction

The beautiful western prairie fringed orchid, *Platanthera praeclara*, was once widespread in the tallgrass prairies across the upper Midwest (Sheviak and Bowles 1986). As Europeans settled North America, they discovered the fertile soils that lay beneath tallgrass prairies and began converting these vast grasslands into agricultural cropland. Some prairie lands were spared the plow only to be altered instead by suppression of the historic fire regimes that had maintained the prairie community for thousands of years. Today, only one percent of original tallgrass prairie remains, mostly in small, relatively isolated fragments, often surrounded by agricultural lands and urban development, and many are further threatened by invasion of non-native species and native woody species that now thrive in the fire-free environment (Kline 1997). Many of the unique plant species of the tallgrass prairie community, including *P. praeclara*, have also suffered great population declines in response to the loss of suitable habitat. The western and eastern prairie fringed orchids, *P. praeclara* and *P. leucophaea*, have declined by more than 70%, according to original county records (Bowles 1983), and therefore in 1989 they were listed as a federally threatened species under the Endangered Species Act (U.S. Fish and Wildlife Service 1996). Habitat loss is considered the greatest threat to the prairie fringed orchids, therefore current management plans focus primarily on maintaining quality prairie habitat using standard restoration techniques, such as burning and mowing (U.S. Fish and Wildlife Service 1996).

Although the survival of *P. praeclara* depends on the preservation and restoration of diverse prairie, habitat conservation alone may not be sufficient for maintaining *P. praeclara* populations over time. Reproduction in some surviving *P. praeclara* populations appears to be limited by low rates of seed set, possibly due to low densities of pollinators or inefficient pollination activity. Pollination of *P. praeclara* appears to be limited to only a few species of hawkmoths (Sphingidae) (Bowles 1983, Sheviak and Bowles 1986), which some suspect are declining in numbers or at least being prevented from reaching orchid populations, possibly due to habitat fragmentation and pesticide use—factors that have contributed to the decline of native bee species (Kearns et al. 1998, U.S. Fish and Wildlife Service). It is important to thoroughly understand the relationship of *P. praeclara* with its pollinator species, because very different restoration and management strategies may be appropriate depending on the status of this pollination interaction. This orchid-hawkmoth pollination relationship has been the subject of research for two decades, but it is still poorly understood and there continues to be much controversy about the status of pollinator hawkmoth species. The example of *P. praeclara* and its pollinators demonstrates the complexities in developing restoration and management strategies for rare and threatened plant species.

Description, distribution and status of *Platanthera praeclara*

The western prairie fringed orchid and its sister species, the eastern prairie fringed orchid, *P. leucophaea*, are among the showiest plants in the *Platanthera* genus and two of only a few orchid species characteristic of Midwestern prairies (Sheviak and Bowles 1986). *P. praeclara* is a smooth, erect,

perennial with a flowering stalk reaching up to 1.2 meters in height and producing 5-25 large (2.5 cm-wide) flowers (U.S. Fish and Wildlife Service 1996). The beauty of the flower is reflected in the epithet “*praeclara*” which was “chosen for its singularly appropriate series of translations: very bright, beautiful, splendid, glorious, distinguished, noble” (Sheviak and Bowles 1986). The flowers of *P. praeclara* are creamy white and deeply fringed with subtly green-hued sepals and a sweet, delicate fragrance that becomes stronger after nightfall, when its hawkmoth pollinators are active (Bowles 1983, Sheviak and Bowles 1986).

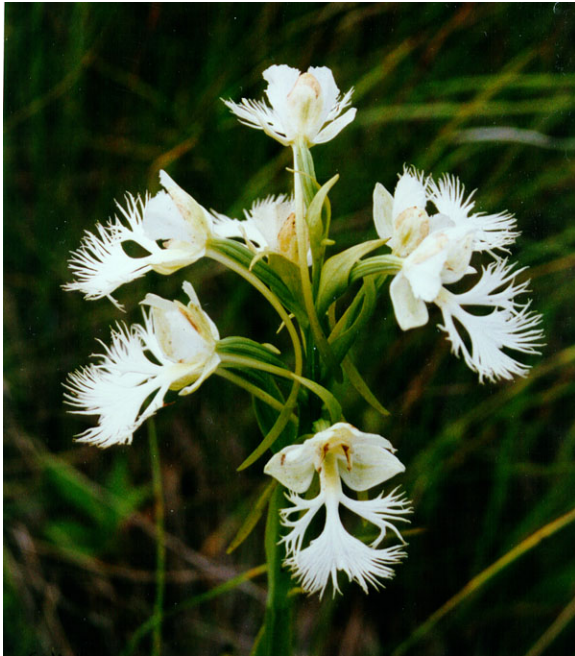


Figure 1. *Platanthera praeclara* in bloom
Photograph by George Nelson Rysgaard

In 1986 *P. praeclara* was recognized as a distinct species and separated from *P. leucophaea*, which inhabits prairies, fens, bogs and wet meadows in the prairie peninsula east of the Mississippi River (primarily in Wisconsin, Illinois, and Michigan), when significant differences were discovered in their morphology and pollination mechanisms. *P. leucophaea* may have evolved from its western relative as it followed the post-glacial northeastward expansion of the prairie peninsula and became adapted to a more diverse range of sites and pollinators. *P. praeclara*, on the other hand, are limited to more undisturbed mesic to wet calcareous prairie habitats, which suggests that preserving high quality prairie habitat is particularly important for conservation and restoration of *P. praeclara* populations (Sheviak and Bowles 1986).

Historically, *P. praeclara* was distributed throughout wet tallgrass prairie swales west of the Mississippi River. Currently there are *P. praeclara* populations in 175 sites in 41 counties in six states (Iowa, Kansas, Minnesota, Missouri, Nebraska, and North Dakota) and Manitoba, Canada (U.S. Fish and Wildlife Service 1996). The majority are located in the northern part of the range, in Manitoba, Minnesota, and North Dakota. The largest remaining populations of *P. praeclara* number in the thousands and are located in sedge-dominated, wet-mesic, prairie swales in northwest Minnesota; grass-dominated, mesic, sand prairie swales in North Dakota’s Sheyenne National Grassland; and tallgrass prairie remnants in southeast Manitoba, all of which are located within the Red River Valley ecoregion (Bowles 1983, Cuthrell 1994, U.S. Fish and Wildlife Service 1996, Portman 2003). These three regions have the largest remaining populations, thus they are especially important locations for restoration and conservation of *P. praeclara*, because they may have the best survival chances for the species, and they also provide greater

opportunity to study pollination and effects of restoration and management techniques on orchid populations.

Only 3% of remaining *P. praeclara* are located in the southern part of the range, and most of these populations are very small and isolated; for example, no populations in Kansas or Missouri, and few in Iowa, contain more than 50 individuals, and many contain fewer than 20 individuals (U.S. Fish and Wildlife Service 1996; M. Leoschke, personal communication). The species is apparently extirpated from South Dakota and Oklahoma. Based on historical records, it appears that *P. praeclara* has been lost from at least 75% of counties in which it was originally recorded. Its 1989 federal listing led to increased interest in locating populations, and subsequently it has been found in more than 28 counties for which there are no historical records. However, these populations are probably not actually new, but simply went unrecorded until *P. praeclara* became a species of interest (U.S. Fish and Wildlife Service 1996; N. Sather, personal communication).

The decline of *P. praeclara* can be attributed primarily to the drainage and direct loss of the tallgrass prairie habitat due to agricultural and later urban expansion. Current threats to the remaining populations include illegal collection of the plants (Bowles 1983), insect herbivory, particularly on developing flowers (Cuthrell 1994; G. Fauske, personal communication), drainage and disturbance of hydrological regimes, competition with invasive species such as *Euphorbia esula* (leafy spurge) (U.S. Fish and Wildlife Service 1996), low pollination rates (N. Sather, personal communication), and potential inbreeding effects from small population sizes and limited pollination (Bowles et al. 2002, Wallace 2003).

The *Platanthera praeclara*-hawkmoth pollination interaction

There are two main players in a pollination event—pollinator and plant—and they each have different goals. The pollinator, in this case a hawkmoth, attempts to locate and obtain the flower's nectar which it consumes as food. The flower, an orchid in this case, produces the nectar to attract hawkmoths, who, in their efforts to reach the nectar contained within the flower's spur, inadvertently brush up against the packets of pollen called pollinia (singular: pollinium) located on the flower's viscidia, the tip of the column formed by the fused stamen and style. The pollinia then stick to the hawkmoth's body, and when it flies to another *P. praeclara* flower, pollen granules may be successfully transferred to the stigma, and thus pollination occurs (Bowles 1983, Sheviak and Bowles 1986, Cuthrell 1994). In general, the plant's ideal evolutionary strategy is to have reproductive structures that are configured in such a way as to only allow nectar access to those insects which will pick up their pollen and act as effective pollinators. If an insect gains access to the nectar without transferring pollen, then it is a net loss of resources for the plant. The insect, on the other hand, is concerned only with reaching and consuming the nectar; it picks up the pollen inadvertently at no direct cost or benefit to itself.

Many plant species are generalists, pollinated by a wide range of insects or by the wind; reproduction in generalists is seldom limited by pollination, and thus these species are more commonly selected for prairie restoration efforts (C. Reed, personal communication). Other plants, on the other hand, are pollinator-specific, which means only a very few species are able to both access its nectar and effectively transfer its pollen to another individual of the same plant species. Similarly, some pollinators are generalists, visiting and obtaining nectar from a variety of plant species, whereas others are specialists and feed only on a very few structurally similar plant species (Sheviak and Bowles 1986).

P. praeclara appears to be pollinator-specific, dependent on only a few hawkmoth species for pollination, whereas its hawkmoth pollinators can obtain nectar from a variety of plant species (Bowles 1983; Cuthrell 1994; B. Stotts, personal communication; C. Jordan, personal communication; G. Fauske, personal communication). The flowers of *P. praeclara* exhibit features typical of sphingophilous (hawkmoth-pollinated) plants: they are large and showy, they lack colored nectar guides, they have deep

spurs containing large amounts of fragrant nectar, and their scent is strongest at night, when moths are active. The spurs that contain the nectar are longer than in any other north temperate *Platanthera* species, extending up to 5 centimeters in length. The corresponding pollinator hawkmoths must have a long enough proboscis to reach the nectar, but it cannot be so long as to avoid contact with the orchid's pollinia. If contact is made, the pollinia generally attach to the hawkmoth's eyes (Bowles 1983, Sheviak and Bowles 1986). Thus, the width across the eyes of an effective pollinator must correspond with the distance between the orchid's viscidia, on which the pollinia are located. Moths with a proboscis longer than *P. praeclara*'s spurs and with a shorter distance across the eyes than distance between the orchid's viscidia will only be "nectar thieves" and not serve as effective pollinators (Sheviak and Bowles 1986).

P. praeclara are facultative outcrossers, which means they can produce seeds through self-pollination as well as through outcrossing with other individuals (Bowles 1983). However, out-crossing is an important strategy for maintaining genetic diversity and avoiding inbreeding depression in a population (Campbell 1993), and it is encouraged in *P. praeclara* via a 60-second delay before pollinia rotate to the position required for attaching to the stigma (Bowles 1983). Hand pollination studies in *P. leucophaea* have demonstrated that outcrossing between and within populations results in considerably higher production of viable seeds (70% and 50% respectively) than does self-pollination (0-15% viable seeds). Small populations may have higher rates of selfing as a result of pollinators revisiting the same flower multiple times, and this could potentially lead to inbreeding depression. In *P. leucophaea*, inbreeding appeared to lead to decreased percentages of seed capsules formation, seed viability, and germination rates (Bowles et al. 2002).

Clearly *P. praeclara* depends on outcrossing pollination for reproduction, however, low pollination rates and seed production have been observed in several populations (Portman 2003; N. Sather, personal communication). Studies have demonstrated that *P. praeclara* is capable of producing a large number of seeds when pollinated (Bowles 1983, Sheviak and Bowles 1986), which suggests that the problem may be a lack of pollinators or pollination activity in orchid populations. If this is the case, a reasonable strategy for managing *P. praeclara* would be to restore this pollination interaction so that existing orchid populations could increase in size and perhaps even expand their current ranges.

Challenges in assessing pollination activity

Before such strategies are developed and implemented, the status of the orchid-hawkmoth pollination interaction must be more clearly understood. Unfortunately, pollination of prairie fringed orchids is a tremendous challenge to study because of the difficulty of observing fast-flying moths at night. During a study of pollination in *P. praeclara* and *P. leucophaea* from 1979 to 1983, only three hawkmoth visitations were recorded, even when ultra-violet lights and red-filtered lanterns were employed to improve visibility (Sheviak and Bowles 1986). In a more recent attempt to survey *P. leucophaea* pollinators in Wisconsin, only 25 hawkmoths were observed in nearly 222 hours of observation time (including 36 hours with blacklight), and of these, only two specimens were found carrying orchid pollinia (Crosson et al. 1999). Observing visitation is not enough to say that a given species is a pollinator; the moths must be caught to determine if it is carrying orchid pollinia, at which point it is considered a pollen vector, or if it visited the flower without picking up the pollinia. A lab study of pollination under controlled conditions found that the long-tongued hawkmoth *Manduca sexta* effectively removed pollinia from *P. leucophaea*, but in all but one case (in which the individual had an abnormally short proboscis) obtained nectar from *P. praeclara* without removing pollinia. Similarly, in a field observation of a population of *P. praeclara* in Adair County, Iowa, flowers contained low nectar levels, indicating moth visitation, but pollinia did not appear to be removed, thus nectar thievery may be a common event for *P. praeclara* (Sheviak and Bowles 1986).

Once a hawkmoth is discovered carrying *P. praeclara* pollinia, it is confirmed as a pollen-vector. At this point its pollinator status is often assumed, but it is important to keep in mind that to this day, an actual pollination event has never been observed in *P. praeclara* (C. Jordan, personal communication). The longhorn beetle, *Typocerus confluens*, has been observed consuming *P. praeclara* pollinia, which is another reason that one cannot use pollinia removal as evidence of pollination in *P. praeclara*. Whether these beetles themselves could act as pollinators is a question that requires further research (Cuthrell 1994).

Because of the difficulties in recording actual pollination events, rates of pollination are often determined by measuring fruit/seed set in orchid populations. Two sites in the Sheyenne National Grassland, ND had seed set rates of only 20% (and these may have had increased pollination levels as a result of using light traps to catch moths in the site), and another site had only 9% fruit set (though orchids in this site may have been affected by local herbicide application) (Cuthrell 1994), indicating fairly low rates of pollination, although more recent studies found pollination rates around 30-40% (Pleasants and Moe 1993; C. Jordan, personal communication). Seed set percentages were even more alarming in Manitoba's vast populations. Studies in the Tall Grass Prairie Preserve, home to nearly all of Manitoba's *P. praeclara*, found that only 2.1% of orchids produced seed. Many factors could explain this low seed set, so researchers Christie Borkowsky and Richard Westwood of the University of Winnipeg designed an experiment to determine whether a lack of pollination activity was the cause. Black lights were used to illuminate the orchid populations at night and attract hawkmoths to the site, and as result, the rates of seed set in these populations increased (Portman 2003), indicating that low rates of seed set in Manitoba were due at least in part to low abundances of pollinators, at least on a very local scale. Small populations have been known to fail completely to set fruit, and because vegetative reproduction is minimal in this species, such populations may be unable to produce new individuals and therefore may not be self-sustaining (Bowles 1983). Based on the findings in North Dakota and Manitoba, even large metapopulations of orchids may currently be unsustainable, due at least in part to a failure in the pollination interaction.

Concerns about low rates of seed set in *P. praeclara* populations have made identifying pollinator species a research priority (U.S. Fish and Wildlife Service 1996), but although pollen vectors for *P. leucophaea* were identified as early as 1964, the pollen vectors for *P. praeclara* have proven to be more elusive (Sheviak and Bowles 1986). In an early study, Sheviak and Bowles (1986) listed four hawkmoth species that, based on measurements of proboscis and eye width, appeared to be potential pollinators for *P. praeclara*: *Eumorpha achemon* (Drury), *Hyles lineata* (F.), *Sphinx drupiferarum* J.E. Smith, and *S. kalmiae* J. E. Smith. Two of these species, *E. achemon* (achemon sphinx) and *S. drupiferarum* (wild cherry sphinx) were eventually confirmed to be *P. praeclara* pollen vectors when, in a 1992-1993 study at the Sheyenne National Grassland, pollinia were found attached to the eye of a museum specimen of *S. drupiferarum* (collected from Ransom County, North Dakota in 1962) as well as single field specimens of *S. drupiferarum* and *E. achemon*. In the course of this study, several other potential pollinators were identified based on proboscis length and eye-width, including *S. gordius*, *S. vashti*, *S. luscitiosa*, *Darapsa pholus*, and *Hyles galli* (Cuthrell 1994). Since then, *H. galli* and *S. eremitus* have been found in light traps or cone traps near flowering *P. praeclara* in ND sites, but have not yet been found carrying *P. praeclara* pollinia (G. Fauske, personal communication).

In studies by Christie Borkowsky, *S. drupiferarum* has also been identified as a pollen vector for *P. praeclara* in Manitoba's Tall Grass Prairie Preserve, as has *H. galli* (bedstraw hawkmoth or gallium sphinx) (Portman 2003; G. Fauske, personal communication). And just this past year, two additional pollen vector species have been confirmed: David Ashley of Missouri Western State College found *Paratraea plebeja* (plebeian sphinx) carrying *P. praeclara* pollen at Tarkio Prairie, Missouri (N. Sather, personal communication), and *Hyles euphorbiae* (leafy spurge hawkmoth) was discovered with orchid pollen in Sheyenne National Grassland, ND (C. Jordan, personal communication). Surprisingly, *H. euphorbiae* is not native to North America but was introduced to North Dakota as a biocontrol agent for

the noxious weed leafy spurge (*Euphorbia esula*) in the 1980s. It was the first insect imported for this purpose and did not establish well on the first several introduction efforts. It was later reported in North Dakota in the early 1990s, and since then, its numbers have increased along with the rapid spread of leafy spurge in North Dakota's grasslands (B. Stotts, personal communication; C. Jordan, personal communication). More effective biocontrol species have since been introduced (C. Jordan, personal communication), but *H. euphorbiae* may prove to be a beneficial species for *P. praeclara*, by helping to decrease the abundance of highly competitive leafy spurge, potentially decreasing the amount of herbicide required, and by providing pollination services. Further observations and research on this new hawkmoth species is certainly warranted.

As the search for pollinators continues, it is important to keep in mind that some pollinator species may pollinate *P. praeclara* more efficiently than others. For example, of the two pollen vector species identified by Christie Borkowsky in Manitoba, *H. galli* is the more common species, but it is also smaller in size than *S. drupiferarum* and may therefore pollinate Manitoba's orchids less efficiently (Portman 2003). Most pollen vectors have been identified based on the observation of only one or a few individuals carrying *P. praeclara* pollinia; whether they are the most effective and efficient pollinators available to orchid populations is unknown.

As a result of continued research and improvements in hawkmoth trapping methods, more *P. praeclara* pollen vectors are being identified, which may ultimately disprove the previously held belief that *P. praeclara* has a very specific pollination relationship with only a few hawkmoth species. It now appears that the specific morphological requirements of *P. praeclara* pollinators are actually met by a several different hawkmoth species, and that a close evolutionary association between prairie orchids and specific hawkmoth species does not exist (G. Fauske, personal communication). Some researchers argue that restoration of pollinator hawkmoth species is unnecessary and misguided, because the species that have been identified are all relatively common and widespread throughout *P. praeclara*'s range and beyond (C. Jordan, personal communication; G. Fauske, personal communication). For example, *S. drupiferarum* is widely distributed across North America, from Nova Scotia southward to Georgia, across the upper Midwest, and west to California. In North Dakota, it is most commonly detected during late June to mid-July, which corresponds with the peak flowering period of *P. praeclara*. *E. achemon* is also widely distributed across the east coast of the United States and west to North Dakota and Arizona. Like *S. drupiferarum*, it is most commonly collected in North Dakota in July, although sporadic collections occur from June through August (Cuthrell 1994).

Furthermore, the hawkmoths' food source plants (for both larvae and adults) also appear to be very common and widespread (C. Jordan, personal communication; G. Fauske, personal communication). As noted previously, hawkmoths are generalists and feed on the nectar of a variety of plants, including *Lonicera dioica* L. (wild honeysuckle), *L. tatarica* L. (tartarian honeysuckle), *Datura stramonium* L. (jimson weed), and *Oenothera* spp. (primroses) (Cuthrell 1994). *E. achemon* caterpillars feed on wild grape (*Vitis* spp.); *S. drupiferarum* caterpillars feed on the foliage of cherry, plum and apple trees; *H. galli* caterpillars feed on bedstraw (*Gallium* spp.) and evening primrose (*Oenothera* spp.), and of course, *H. euphorbiae* feeds on the very abundant leafy spurge (although both of these are introduced species) (C. Jordan, personal communication). If pollination is limiting in *P. praeclara* populations, it is not likely due to a lack of suitable food sources for pollinating hawkmoth species.

A final argument against the hypothesis that *P. praeclara* is limited by pollinator abundance is that hawkmoths are capable of traveling very long distances (Cuthrell 1994; C. Jordan, personal communication; G. Fauske, personal communication). The individuals that pollinate orchids in North Dakota may be local residents or long-distance immigrants from the southern United States (Cuthrell 1994; U.S. Fish and Wildlife Service 1996; G. Fauske, personal communication). Because of their long-

distance flying capacity, it would seem unlikely that habitat fragmentation limits local abundance of hawkmoths or their ability to reach orchid populations (C. Jordan, personal communication).

Clearly there is still much to be learned about the status of the orchid-hawkmoth pollination interaction. Although none of the identified pollen vectors are considered threatened, and no studies have been conducted that demonstrate population decline, the fact remains that seed production and hence pollination activity is low in a large number of *P. praeclara* populations. Hawkmoth densities and pollination rates in *P. praeclara* populations are still largely unknown (U.S. Fish and Wildlife Service 1996), and it may be that whatever phenomenon is occurring is doing so at very local scales.

Challenges in assessing *P. praeclara* status and threats

Research and monitoring of *P. praeclara* and its associated hawkmoth populations is necessary to determine whether reproduction of *P. praeclara* is limited by pollination rates, and if so, how and why? Monitoring pollination events poses many challenges, as described previously, and monitoring *P. praeclara* populations has also proven to be very difficult, primarily because the visible individuals are highly variable due to periods of dormancy and irregular flowering. According to some sources, *P. praeclara* are long-lived with periods of dormancy (Bowles 1983), while other reports seem to indicate variable life-spans affected by soil moisture and other factors (U.S. Fish and Wildlife Service 1996). Permanent transects were established in orchid populations in Sheyenne National Grassland in order to monitor individual orchids and populations over time. In 1987, 160 orchid plants were tagged, and by 1994 only four percent of tagged orchids remained in the population; most of the tagged plants disappeared after only one or two growing seasons, never to reappear. This study indicates that while *P. praeclara* are capable of living up to eight years, they generally live only a few years, at least if they are subjected to periods of drought, as they were in the early 1990s (Sieg and King 1995; Sieg 1997; B. Stotts, personal communication). This may be especially significant in small populations which are already failing to produce new individuals because of low pollination rates (or other factors), because in adverse environmental conditions, existing plants may fail to regenerate themselves as well, leading to complete population decline.

Erratic flowering patterns also make *P. praeclara* a challenge to monitor, because it is difficult to locate non-flowering individuals. In some years, an orchid may send up only one to three leaves, while in other years it will produce a tall, very visible flowering stalk (Bowles 1983, Portman 2003). Periods of dormancy and erratic flowering in *P. praeclara* make long-term monitoring of populations essential, because a census in any one year may not be an accurate representation of the true number of individuals in a population. Small populations may go undetected, and numbers of large populations may fluctuate dramatically from year to year. Observation records show large fluctuations in nearly every Minnesota *P. praeclara* population; for example, the following population fluctuations were reported in a *P. praeclara* population in Pembina Trail Preserve, northwest Minnesota: 1990: 50 individuals; 1993: 382 individuals; 1994: 1001 individuals; 1995: 933 individuals; 1996: 1302 individuals; 2001: 343 individuals; 2002: 204 individuals (unpublished data, Natural Heritage Information System, Minnesota Department of Natural Resources). In fact, Manitoba's population was unknown to science until 1984, despite being the largest extant population in North America! Since the "discovery", surveys of the Manitoba population have found as few as 1,800 individual orchids, and in 1997, a record high of 21,000 flowering individuals were counted. This year (2003) was another moist year in Manitoba, and researcher Christie Borkowsky estimates the orchids numbered nearly 20,000 (Portman 2003).

Periods of dormancy and years with reduced vegetative growth and flower production may be an adaptive strategy by which the orchids are able to survive in the drought- and fire-prone prairies (Bowles 1983; B. Stotts, personal communication). Recent studies indicate that soil moisture is one of the most significant influences on orchid numbers and flowering (Sieg and King 1995; Portman 2003; B. Stotts, personal

communication). In the wettest years with abundant rainfall and a high water table, orchid populations in Sheyenne National Grassland may exceed 10,000 individuals, but in drought years, numbers are dramatically reduced, and orchids may only be found in the deepest, moistest swales (Sieg and King 1995; Sieg 1997; B. Stotts, personal communication). Currently soil water levels are being monitored near *P. praeclara* populations at the Sheyenne National Grassland to try and clarify these population trends (B. Stotts, personal communication). The western distribution of *P. praeclara* is probably limited by moisture levels (Bowles 1983), and the future of the species may be impacted by global warming if there is no way for the species to disperse and establish to new locations in a sufficiently moist climate.

Potential threats to the *P. praeclara*-hawkmoth pollination interaction

These periods of dormancy and reduced flower production not only make it difficult for humans to locate and study *P. praeclara*, they may also contribute to reduced numbers of pollinators in the orchid populations. As previously described, hawkmoths are widely distributed, feed on the nectar of many common plant species, and can travel long distances to locate food sources, which would seem to support the argument that pollinator abundances do not limit reproduction in *P. praeclara* populations. However, their distribution may not be even over time and space; they may concentrate their time in areas with the biggest nectar payoffs, and only visit *P. praeclara* populations that are large enough to provide a nectar source comparable to other plant populations. This would mean that *P. praeclara* are essentially competing with other hawkmoth-pollinated plant species for these important pollination services (Bowles 1983; B. Stotts, personal communication). Small and sparse populations of *P. praeclara* may be thus be at even greater risk of pollination limitation, and in years where most orchids are dormant, any individuals that do flower may have a reduced chance of being pollinated, because fewer pollinators will be attracted to the area, and other individuals with which the pollen may be transferred will be sparsely distributed. If hawkmoths are distributed patchily and *P. praeclara* populations are being out-competed by other hawkmoth-pollinated species, the densities and distributions of hawkmoth nectar sources may need to be assessed and incorporated into management plans.

Population size of *P. praeclara* may not be the only factor influencing pollination rates. In fact, a study of pollination at the Sheyenne National Grassland found that pollination rates were not significantly higher at large populations than small populations (Pleasants and Moe 1993). The extreme isolation of most *P. praeclara* populations, and the fragmentation of the surrounding landscape may prevent pollinator species from reaching them (Kearns et al. 1998; U.S. Fish and Wildlife Service). Even pollinators that travel long distances may be unable to cross large expanses of croplands if those crop fields are frequently sprayed with pesticides. Pollination rates in Minnesota's *P. praeclara* populations are very low, and contrary to what one might assume, they appear to be even lower in the huge populations of northern Minnesota than in the smaller populations of southwestern Minnesota and Iowa (N. Sather, personal communication). This may be evidence of a regional decline in actual numbers of hawkmoth pollinators, or simply a result of the lower densities of hawkmoths at the northernmost parts of their range (Portman 2003; C. Jordan, personal communication), or it may be due to an inability to cross crop fields surrounding *P. praeclara* populations.

Ongoing studies at Sheyenne National Grassland continue to try to elucidate the relationship between *P. praeclara* population size and pollination rates (G. Fauske, personal communication; C. Jordan, personal communication). An interesting observation that deserves further research is that the large populations in northern Minnesota and Sheyenne National Grassland, ND occur in areas of high potato production, while smaller populations in Iowa are not surrounded by potato fields. These potato fields are regularly sprayed with pesticide to control a pest hawkmoth, tobacco hornworm (*Manduca sexta*), which is a species identified as a possible pollinator (or nectar thief) of *P. praeclara*. It would be interesting to determine whether pollination rates are lower in *P. praeclara* populations surrounded by potato fields than in other regions, because it may be that the pesticide used in adjacent lands is affecting pollination rates, either by

eliminating *M. sexta*, a potential pollinator, or possibly even by reducing numbers of other known pollinator species (N. Sather, personal communication). The 2500 acre Tall Grass Prairie Preserve in Manitoba is not surrounded by potato fields, but it is composed of a series of eighth and quarter sections among pasture lands and agricultural fields of alfalfa, corn and oats (Portman 2003). Perhaps this fragmentation and pesticide use in surrounding lands could explain the extremely low pollination rates in Manitoba's *P. praeclara* populations. Pesticide use has also been raised as a potential concern for *P. leucophaea*'s pollinator species in Illinois (Vitt 2001; K. Lah, personal communication). As with *P. praeclara*, very little is known about the status and numbers of *P. leucophaea*'s pollinators, but some researchers are worried that general pesticide application for gypsy moth control may be having an impact on orchid-pollinating hawkmoths, and this may contribute to the low natural pollination rates observed in *P. leucophaea* populations (K. Lah, personal communication).

Even if hawkmoths are abundant throughout much of their range, something may be preventing them from being attracted to orchid populations during the critical flowering period. This may be pesticide use in the surrounding landscape, as just discussed; it may be due to an inability of orchid populations to compete with other nectar sources; or, at least in some cases, it may also be due to a mismatch in timing of moth presence and orchid flowering. In Manitoba—the northernmost part of both *P. praeclara* and many hawkmoth ranges—the two identified pollen vectors, *S. drupiferarum* and *H. galli* are nearing the end of their lifespans by *P. praeclara*'s peak flowering time in mid-July, and therefore it is possible that fewer moths are flying through the orchid population during that critical period (Portman 2003). Simply determining that pollinator species are present in orchid populations at some point during the year is inadequate; it is whether they are present in sufficient densities during the flowering period that really matters. If mismatched timing is the reason for low pollination rates in Manitoba's *P. praeclara* populations, many further questions arise: Is the mismatch a historical phenomenon? If so, how did *P. praeclara* compensate for these low pollination rates in the past? Or were orchids and pollinators both present in higher abundances in the past and therefore the timing issue was minimized? If this is a relatively new problem for *P. praeclara*, is it because another better-matched pollinator species is no longer available to provide pollination services? Or perhaps either flowering periods or hawkmoth lifespans have shifted or changed over time, as a result of climate change or landscape alterations. The current and historical relationship between *P. praeclara* and its pollinators is still far from clear.

Current management strategies and pollinator research

To effectively manage *P. praeclara*, its life cycle and pollination requirements must be understood and taken into account. Two general strategies that have been suggested are: 1) maintenance of large populations, such as those located in Minnesota, North Dakota and Manitoba, and 2) restoration of smaller populations, so that they have a better chance of attracting pollinators, maintaining genetic diversity and withstanding environmental fluctuations and disturbance. Another important area of research is characterizing and identifying suitable habitat for orchid reintroduction (Sieg and King 1995, Sieg 1997). Strategies for large populations have focused on preserving prairie habitat, but low seed set rates in large populations indicate that pollination limitation may not just be a concern for small populations. Large, small, and reintroduced populations of *P. praeclara* will all have a better chance of long-term survival if their natural reproductive cycles are intact, although they may need a boost from humans in the short-term, including techniques such artificial outcrossing pollination (Bowles 1983).

Loss of habitat is the greatest overall threat to *P. praeclara*, therefore the U.S. Fish and Wildlife Service recovery plan (1996) states that “the best management for this species is likely to be that which maintains the quality of the grassland and prairie habitats”. In general, management of *P. praeclara* populations has utilized standard prairie management practices and has focused on maintaining and expanding prairie habitat, identifying suitable habitat for orchid reintroduction, and continuing research and monitoring (U.S. Fish and Wildlife 1996). Burning is one of the most common tools for managing the orchid's prairie

habitat. In Iowa, only portions of the orchid's prairie habitat are burned in a given year (M. Leoschke, personal communication), and in Minnesota, most orchid populations on public lands are managed with a standard 3-4 year burn rotation of spring and fall burns (N. Sather, personal communication). Timing is critical: fire appears to stimulate flowering, but burns, mowing and grazing can all have either beneficial or detrimental effects depending on the stage of the orchid life cycle in which they occur and the environmental conditions at the time (Bowles 1983, U.S. Fish and Wildlife Service 1996). For example, it appears that burns during the last week in May, which are standard for private seed producers, may actually prevent orchids from flowering for at least one year and possibly several; it is unknown whether these later spring burns may actually kill orchids that have already emerged (N. Sather, personal communication). Thus it is advised that burns in areas of orchid populations occur in early spring, before orchid emergence, or late fall, after senescence. Similar recommendations are made for mowing regimes in order to avoid damaging orchids and preventing seed set and maturation (Cuthrell 1994).

Annual climatic patterns may also impact the effectiveness of various management strategies. For example, a dormant-season burn might reduce flowering if it occurred in a dry year and there was insufficient precipitation to replace soil moisture lost from the fire. The combination of fire and favorable environmental conditions may result in the highest flower production. Mass flowering events have been observed after mowing has been eliminated and a burn regime initiated (Bowles 1983), although some amount of mowing can reduce light competition and actually benefit orchids. Preliminary phenological observations in mowed and unmowed plots in Minnesota in 2003 suggest that orchids tend to emerge one week earlier in mowed areas than in areas with standing litter (N. Sather, personal communication). Elimination of grazing has also been known to lead to sudden appearances of *P. praeclara* where it was not previously observed, although moderate grazing may benefit the orchid by reducing competition for light (Bowles 1983).

Sheyenne National Grassland, home of North Dakota's only remaining *P. praeclara* population, is an excellent location for researching the impacts of management strategies on orchid populations. The grasslands are multi-use lands with a management regime that includes seasonal mowing, grazing, and burning (Bowles 1983; Sieg and King 1995; Sieg 1997; B. Stotts, personal communication). As a threatened species, *P. praeclara* factors into management plans, but the land as a whole is not managed specifically for the orchid (B. Stotts, personal communication). The restoration and management goal is to increase the size of local prairie remnants to keep pollinators (and other requirements) for the species in place (B. Winter, personal communication). The populations of *P. praeclara* have been monitored to try and determine the impacts of various combinations of management treatments—including grazing, burning, combined grazing and burning, and neither grazing or burning—on both orchid numbers and seed set rates. The research is ongoing, but thus far, although orchid populations have fluctuated dramatically during the management period, no direct effects of the various management strategies on population numbers have been detected (Sieg and King 1995; Sieg 1997; B. Stotts, personal communication; B. Winter, personal communication).

It may also be important to consider the impacts of prairie restoration and management regimes on the local distribution of pollinator hawkmoth species. Fire and mowing are both used to maintain diverse, open prairie habitats and prevent succession to woodland, because orchids, like many prairie species, cannot compete with woody species for light (Bowles 1983). However there is some evidence that hawkmoth pollinators of *P. praeclara* utilize nearby woody species in lowlands and river bottoms as daytime refuges, indicating that it may be important to maintain some woody cover to encourage the presence of pollinators in and around orchid populations (N. Sather, personal communication; B. Stotts, personal communication).

Managing the prairie habitat for orchid populations is clearly the highest priority restoration strategy, however, low natural pollination rates even in large populations has led to the development of methods to

boost reproductive capacity. Artificial pollination techniques have been employed in populations of eastern prairie fringed orchid, *P. leucophaea*, in Illinois where it is listed as endangered, ever since it was discovered that populations were failing to set seed even in protected habitats, suggesting that natural pollination rates by hawkmoths were low (Keibler 1997; M. Bowles, personal communication). Artificial pollination has become a formal restoration project in Illinois, run by The Nature Conservancy and the Fish and Wildlife Service, in which volunteers are trained in hand-pollination and census taking of existing orchid populations. After three consecutive years of hand pollinating, orchids that out-crossed via hand-pollination had higher viable seed production than in natural hawkmoth pollination (nearly twice the percentage, in fact). This is likely due to the fact that in hand-pollination, the entire pollinium (pollen packet) can be deposited on the orchid's stigma, maximizing the number of pollen available to the plant for seed production, whereas in natural pollination, the pollinia typically remain attached to the insect and only a few pollen grains are deposited (Bowles et al. 2002; M. Bowles, personal communication).

The seeds produced by hand-pollinated *P. leucophaea* are collected and dispersed to additional sites in Illinois, including current populations, sites where historical populations have been lost, and sites in suitable habitat in which no population has been recorded. Within the first few years, hand-sown seeds produced three individuals growing on a site with no previous record of orchid populations, and several existing populations produced large numbers of flowering plants after brush was cleared from the area (Keibler 1997). By 2002, 43 sites with no previous orchid records had been seeded, four of which have produced orchids (Keibler 2001, Keibler 2002). In addition to their use in restoring *P. leucophaea* populations, the excess seeds produced through artificial pollination methods are used for research of orchid propagation and germination requirements, including symbiotic mycorrhizal fungi relationships (Zettler et al. 2001; Bowles et al. 2002; M. Bowles, personal communication). Artificial pollination has shown promise in restoring *P. leucophaea* populations, and now plans are underway to begin artificial pollination studies in *P. praeclara* as well at Pembina Trail Preserve in western Minnesota (N. Sather, personal communication; P. Vitt, personal communication), and at Sheyenne National Grassland, ND (B. Stotts, personal communication).

However, no research in either species has attempted to restore natural pollination to the orchid populations. Marlin Bowles, Plant Conservation Biologist at the Morton Arboretum in Illinois, describes this as “a real void” in *P. leucophaea* research, because very little is known about the hawkmoths that naturally pollinate these orchids. Potentially, hand-pollinating may be a useful technique for maintaining genetic diversity in small populations in the short term and expanding their numbers over time so that they are better able to attract native pollinators. However, more research is needed, because while hand-pollinating may be a successful short-term solution, the ideal goal of population restoration would be self-sustainability of populations through natural pollination. According to Christie Borkowsky, who has researched pollination in Manitoba's orchid populations, one advantage of attracting natural pollinators to a population rather than using hand pollination techniques is that it is difficult to determine the optimum time to pollinate an orchid, whereas an insect may be able to detect floral cues and visit the flower at the time of peak receptivity to pollination (Portman 2003). Also, using pollination outcrossing as a restoration technique is controversial, because of concerns that it may lead to outcrossing depression—the disruption of locally adapted gene complexes. This may be unlikely, since hawkmoths are long-distance travelers and probably historically contributed to landscape-scale gene flow across prairie fringed orchid ranges, however it warrants further research because of the potential risks posed to extant orchid populations (Bowles et al. 2002).

Additionally, more research is required to ensure that the high levels of seed production that results from hand pollination is not harming the prairie fringed orchids in the long run by imposing too high of a resource cost on individual plants (Bowles et al. 2002). The possibility that prairie fringed orchids may actually be adapted to low pollination rates and could thus be harmed by restoration efforts seeking to increase pollination rates must be considered. In the *P. leucophaea* artificial pollination project, care is

taken to ensure that hand pollination does not cause harm to existing populations. For example, only about one third of the flowers on one third of the plants are hand pollinated in order to minimize negative impacts and leave some pollen for natural pollinators. Also, detailed demographic studies are conducted annually to help ensure that hand pollination is not having a harmful impact on orchid populations (Keibler 2001; Keibler 2002; K. Lah, personal communication). Early results indicate that hand pollinating 70% of flowers on an orchid plant results in smaller plants (plant height and leaf size) in the next growing season than does pollinating 30% of flowers, suggesting that there is a resource cost to high pollination rates (Vitt 2001). Artificial pollination research is only just beginning in *P. praeclara*, so it is not yet known whether the two prairie orchids respond similarly to these pollination techniques. A more thorough understanding of *P. praeclara*'s life history and reproductive strategies is needed so that our restoration techniques do not ultimately do more harm than good.

Conclusion: future recommendations

Although the immediate need for greater pollination rates and better understanding of natural pollinators is widely recognized, as of yet, no restoration and management plans have directly incorporated pollinator needs, and there are no existing projects that are trying to restore natural pollinators to *P. praeclara* populations (N. Sather, personal communication; M. Bowles, personal communication; C. Jordan, personal communication). Whether this is problematic or not depends upon the nature of the orchid-pollinator interaction, and the life history and reproductive strategies of *P. praeclara*. Pollinator surveys in and around orchid populations should continue, in order to identify which hawkmoth species are the most effective and efficient pollinators in the region, and to develop a clearer understanding of their local densities, distribution, and pollination activities. Efforts to determine the cause of observed low pollination rates in *P. praeclara* populations are especially critical. If low pollination rates were the historical norm for prairie fringed orchids, and if pollinator species are at their historical densities in *P. praeclara* populations, then efforts to "restore" hawkmoth species and the pollination interaction may be unnecessary and misguided. Valuable time, energy, and resources may be detracted from more appropriate and effective management strategies, such as determining *P. praeclara*'s exact soil and mycorrhizal fungi requirements, which may affect germination rates and soil seed bank longevity; determining factors that affect plant longevity; and addressing herbivorous depredation on orchid flowers, particularly during dry years (G. Fauske, personal communication). Even efforts to increase pollination rates artificially may be detrimental to orchid survival if they are not adapted to the increased resource output resulting from over-pollinating.

However, if the low rates of pollination in *P. praeclara* populations are anthropogenic in nature, we must determine the exact causes before we can develop effective strategies to remedy the situation. Pollinator hawkmoth species do not appear to be declining in abundance on a regional scale, but it is possible that they are patchily distributed and are failing to visit orchid populations, either because of fragmentation or pesticide use in the surrounding landscape, or because orchid populations are unable to compete with other nectar sources for pollinator services. The most appropriate strategies for encouraging orchid pollination will depend on which of these factors (if any) are contributing to the low pollination rates. For example, if hawkmoth populations are lacking in orchid populations because of nearby pesticide use, it may be most important to work toward reductions in pesticide use or a switch to more species-specific or biocontrol methods in regions around orchid populations. Research that demonstrates the impacts of pesticides on orchid pollinators is necessary, because without this evidence, it is difficult to persuade landowners to use species-specific pesticides, which tend to be more expensive and less effective (K. Lah, personal communication).

If, however, pollinators are failing to visit *P. praeclara* populations because they are choosing to spend their time at other nectar sources, then efforts must be focused on increasing the attraction of orchid population sites to potential pollinators, either by increasing the number of nectar sources in the

immediate vicinity of orchids; by maintaining daytime brush habitat for hawkmoths near orchid populations; or by using artificial methods, such as using blacklights to illuminate orchid populations at night. Research by David Cuthrell in the Sheyenne National Grassland and by Christie Borkowsky and Richard Westwood in Manitoba have found that light-trapping and blacklights increase insect activity in local areas and potentially lead to increased pollination of orchids (Cuthrell 1994, Portman 2003), so perhaps lights could be used as a short term method for attracting natural pollinators to flowering orchid populations in which pollination rates are low.

Although it seems unlikely that the long-distance traveling hawkmoths could be prevented from reaching orchid populations because of landscape fragmentation, perhaps the combination of fragmentation, pesticide use, and competing sources of nectar are all interacting and contributing to low pollination rates in *P. praeclara*. If so, there may be a way to create hawkmoth “habitat corridors” that are free from pesticide use and contain some optimum composition of food source plants, especially between orchid populations that are relatively close together (Kearns et al. 1998; U.S. Fish and Wildlife Service). However, in reality, many *P. praeclara* populations may be too isolated to connect by corridors, and expansion of existing populations may be limited by the surrounding landscape, over which resource managers have little influence (B. Stotts, personal communication).

Effective pollination is vital to the long-term survival of many plant species, and yet it is often poorly understood and seldom is it considered directly in conservation and restoration efforts (Bond 1995). Systems of pollination are increasingly threatened by habitat fragmentation, agricultural practices, use of chemical pesticides and herbicides, and increases in invasive species, as evidenced by recent declines in numbers of native bees and non-native honeybees (Kearns et al. 1998). The western prairie fringed orchid and its hawkmoth pollinators may be one example of this phenomenon, but there is still tremendous uncertainty as to whether there is a problem in the orchid-pollination interaction that even needs to be “fixed”. Very different restoration and management strategies may be appropriate, depending on the answers to this perplexing pollination riddle. Strategies based on incorrect assumptions may at best detract from more effective management methods, and at worst, cause direct harm to *P. praeclara* populations. The complexity and confusion surrounding the beautiful western prairie fringed orchid and its hawkmoth pollinators exemplifies both the challenge and the necessity of incorporating a more complete understanding of plant-pollinator interactions into restoration and management plans for all our rare and wonderful plant species.

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